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Predator occurrence and perceived predation risk determine grouping behavior in guanaco (*Lama guanicoe*)

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ABSTRACT

Grouping behavior of social ungulates may depend on both predator occurrence and perceived predation risk associated with habitat structure, reproductive state and density of conspecifics. Over three years, we studied grouping behavior of guanaco (*Lama guanicoe*) families in Chilean Patagonia during the birthing season and determined their response to variation in predator occurrence and perceived predation risk (habitat structure, calf/adult rate and density of conspecifics). We considered the effect of two predators, puma (*Puma concolor*) and culpeo fox (*Lycalopex culpaeus*). We measured two common (family group size and vigilance) and one novel (family group cohesion) behavioral responses of guanaco. Our results show that guanaco family groups adapted their grouping behavior to both predator occurrence and perceived predation risk. Larger family groups were found in open habitats and areas with high puma occurrence, while guanacos stayed in small family groups in areas with

high shrub cover or low visibility. Group cohesion increased in areas with higher occurrence of pumas and culpeo foxes, and also increased in smaller family groups and in areas with low guanaco density. Vigilance (number of vigilant adults) was mainly related to group size and visibility, increasing in areas with low visibility. While residual vigilance (vigilance after removing the group-size effect) did not vary with the explanatory variables examined. Our results suggest that a mix of predator occurrence and perceived predation risk influences guanaco grouping behavior, and highlights the importance of evaluating different antipredator responses together and considering all predator species in studies aimed at understanding ungulate behavior.

KEYWORDS

Group size, landscape of fear, social organisation, ungulates, puma, culpeo fox

INTRODUCTION

Predation risk is one of the main factors that shape grouping behavior in ungulates (Jarman 1974, Kie 1999, Moll et al. 2016). Results from previous studies suggest that prey develop dynamic and complex grouping behaviors as antipredator strategies (Caro et al. 2004, Creel et al. 2014, Moll et al. 2017, Périquet et al. 2017). Grouping behavior can respond to the presence of predators (risky places according to Moll et al. 2016, 2017; Table 1) or to conditions related to habitat structure, conspecific density and group size that influence perceived risk (Laundré et al. 2001; Table 1). Living in groups has additional demonstrable benefits, such as improved predator detection (Pulliam 1973, Lima 1995, Kie 1999), reduced probability of being predated once detected (dilution and confusion effects; Lehtonen and Jaatinen 2016), and less individual time allocated to vigilance (collective vigilance; Lima and Dill 1990, Childress and Lung 2003, Creel et al. 2014). Habitat structure can shape predator-prey interactions through changes in visibility and the presence of either cover refuges or escape

52 impediments (Jarman 1974, Ripple and Beschka 2003, Eccard et al. 2017). In this sense, habitat
53 openness will set the maximum group size, while predation risk will limit the minimum size
54 (Jarman 1974). Finally, Moll et al. (2017) suggested that prey behavior and assessment of risk is
55 modulated by the prevailing conditions (e.g. resource distribution, which also influences group
56 size through intraspecific competition among group members for food; Jarman 1974, Marino
57 2010); and prey characteristics (e.g. presence of offspring, as calves usually are more
58 vulnerable and the preferred prey for predators; Bank et al. 2002, Childress and Lung 2003,
59 Creel and Winnie 2005, Tambling et al. 2012; Table 1).

60 Guanacos (*Lama guanicoe*) are monomorphic ungulates native to South America.
61 Guanacos have a polygynous resource-defense mating system, and their social organization
62 varies over the course of a year (Franklin 1982, Gonzalez et al. 2006). During the birthing
63 season in late austral spring and early summer, the most common social unit is the family
64 group. Family groups typically consist of a territorial male and several females with their
65 offspring. While the social organization of guanacos has been the focus of much research (e.g.,
66 Franklin 1982, Ortega and Franklin 1995, Acebes et al. 2013, Schroeder et al. 2014),
67 uncertainty remains regarding the influence of predation risk on group formation and the
68 factors that determine composition of family groups. This is because previous studies
69 regarding the effects of predation risk on grouping behavior in guanacos have either been
70 conducted in areas with strongly contrasting predation risk (presence/absence of predators;
71 Marino 2010, Marino and Baldi 2008) or using humans as surrogates of predation risk
72 (Taraborelli et al. 2012, 2014). No studies have evaluated antipredator responses of guanacos
73 to gradual variation in predator occurrence and perceived predation risk.

74 In the Chilean Patagonia, guanacos have two native predators: pumas (*Puma concolor*),
75 the main predators, and culpeo foxes (*Lycalopex culpaeus*). While pumas prey on both young
76 and adult guanacos (Franklin et al. 1999, Bank et al. 2002, Elbroch and Wittmer 2012), culpeo
77 foxes are opportunistic predators of chulengos (guanaco calves up to 1 year in age; Novaro et

78 al. 2009). Responses in social organization and group formation in guanacos should thus
79 depend on predator species. In carnivore-ungulate systems, behavioral studies simultaneously
80 considering the effect of more than one predator species are rare (Thaker et al. 2010, Creel et
81 al. 2017, Moll et al. 2017).

82 We evaluated the grouping behavior of guanaco family groups to predator occurrence
83 and perceived predation risk during the birthing season in an area encompassing both a
84 protected and a non-protected area. The birthing season is considered the most critical period
85 due to the high predation risk experienced by chulengos (Bank et al. 2002). The management
86 of the protected and unprotected area is different. In the first, wildlife is protected and
87 livestock is excluded. While, the surrounding non-protected area is dedicated to extensive
88 livestock and wildlife is often persecuted. Antipredator behavior is a complex and
89 multidimensional process. Univariate analyses may thus lead to contradictory results and the
90 simultaneous use of different behavioral indicators may help develop a comprehensive
91 understanding of this behavior (Creet et al. 2014, Lehtonen and Jaatinen 2016, Moll et al.
92 2017, Cappa et al 2017). For that reason, we quantified several antipredator grouping
93 responses in order to provide a more accurate understanding of how guanacos respond to
94 predation risk: group size, group vigilance, and group cohesion, the last being a novel and easy-
95 to-measure antipredator behavior (Table 1). Group cohesion is considered a measure of risk
96 assessment (Peacor 2003). In the presence of predators, groups of social species become more
97 compact, probably due to the advantages of group defense and avoidance of predators (Lima
98 and Dill 1990). Increasing group cohesion may improve early detection of an approaching
99 predator and thus provide guanacos with longer response time (Taraborelli et al. 2012).

100 We considered responses to both predator occurrence (pumas and culpeo foxes) and
101 perceived predation risk (habitat structure, protected vs. unprotected area, conspecific density
102 and proportion of chulengos in each group). If guanacos respond to predator occurrence, we
103 would expect larger, more cohesive groups as well as higher vigilance in areas with higher

probability of encounter with a predator (Table 2). On the other hand, if guanacos respond to perceived predation risk, which is mainly determined by habitat structure, we would expect smaller, more cohesive groups as well as higher vigilance rates in areas with higher shrub cover and low visibility, because these will be perceived as riskier habitats independent of predator occurrence (Table 2). Due to the large abundance of wildlife within the protected area, we expected larger, more cohesive and more vigilant groups within it than in the non-protected area (Table 2). A higher chulengos/adult ratio potentially increases the perceived risk because chulengos are the preferred predator's prey (Franklin et al. 1999). Thus, we expected an increase in group cohesion and vigilance with increasing proportion of chulengos (Table 2). Finally, it has been suggested that conspecific density relaxes perception of risk through intraspecific communication and risk detection at large distances (Donadio and Buskirk 2006, Creel et al. 2017). We thus also expected an increase in group cohesion and vigilance in areas with lower conspecific density (Table 2).

MATERIAL AND METHODS

Study area

We conducted our study in the Comuna Torres del Paine (51°3'S; 72°55'W) in the Última Esperanza Province, Region of Magallanes, Chile. Study area covered approximately 1090 km^2; 284 km^2 were located within Torres del Paine National Park (TPNP) and 806 km^2 were part of several neighboring private ranches (Fig. 1). Annual rainfall in the area varies between 300 and 1000 mm, and mean temperature ranges from 2.0 °C in winter to 10.8°C in summer (Vidal and Reif 2011). Vegetation is dominated by steppe-like grasslands and shrublands (Pisano 1974). TPNP is separated from surrounding ranches by a 1.2 m high wire fence, which restricts livestock movements from ranches into the National Park but allows wildlife movements, although guanacos occasionally die entangled in it (Rey et al. 2012).

129 Guanacos are the most abundant large-bodied native herbivore in the study area.
130 Estimated guanaco densities currently vary from 36.6 (within TPNP) to 8.8 (outside TPNP)
131 individuals/km^2 (Iranzo et al. 2017). Other medium to large-bodied native herbivores found in
132 our study area are lesser rhea (*Pterocnemia pennata*) and upland geese (*Chloephaga picta*),
133 both of which occur at low densities compared to guanacos. Introduced European hares (*Lepus*
134 *europaeus*) are present throughout the study area and are locally abundant. Pumas and culpeo
135 foxes occur at variable densities throughout the study area. Reported puma densities within
136 TPNP are high compared to density estimates from other areas of their distribution (Franklin et
137 al. 1999, but see Rinehart et al. 2014) and decline towards surrounding areas (own
138 unpublished data). Culpeo foxes within TPNP occur at an estimated density of 1.2
139 individuals/km² (Lucherini 2016), and at a similar density in the surrounding areas (own
140 unpublished data).

141 Data collection

142 We conducted surveys during the birthing season in December (i.e., during late Austral spring)
143 of three consecutive years (2009, 2010 and 2011) to determine size, cohesion and vigilance of
144 guanaco family groups. Two survey teams equipped with binoculars carried out vehicle and
145 foot-based surveys along the existing network of paths and roads in the study area (total
146 transect length surveyed = 336.4 km/year) and recorded all guanacos (individuals and groups)
147 they encountered. Researchers were trained to determine visual estimation criteria in a
148 consistent way. In addition, to reduce possible bias, the members of teams were rotated daily.
149 A detailed description of survey methodology is provided in Iranzo et al. (2013), Iranzo et al.
150 (2017), and Traba et al. (2017).

151 We recorded the GPS position for every family group detected, and determined its
152 size, composition (sex, and age classified as adult, juvenile or chulengo) and location (within or
153 outside protected area). To evaluate group cohesion (a measure of packing or animal density
154 per family group), we visually estimated the occupation area (maximum length and width).

Using instantaneous scan sampling, we quantified the number of adults with heads up (above the shoulder level) at the time of our first observation, avoiding any kind of disturbance by the observers, and used this number as an approximation of group vigilance (Childress and Lung 2003). To assess perceived predation risk, we visually estimated shrub cover and visibility within a 50 m radius around the centroid of the group. Visibility was assessed based on terrain roughness and the presence of rocks or other visual obstacles, and classified into three categories: high (no visual restriction in any direction), medium (reduced visibility in some direction), and low (low visibility in all directions). During surveys, we also recorded the location and size of bachelor groups, female groups and solitary guanacos in order to estimate total guanaco density (Iranzo et al. 2017).

To determine the influence of both predators on guanaco behavior we estimated their relative occurrences in the study area using two complementary methods. First, we conducted snow track surveys during austral winters of 2011 and 2012. Surveys were conducted by two observers walking 200 m linear transects, 5 m width, every 5 km along the same set of roads and paths used to survey guanacos (year 2011: n = 40 transects covering 8km; year 2012: n = 54 transects covering 10.8 km). During surveys, we recorded all signs (i.e., faeces, tracks) of puma and culpeo fox presence. Despite the mismatch between sampling periods, pumas and culpeo foxes occupy distinct home ranges and are relatively long lived; we thus did not expect large differences in either space use or occurrence among years. Moreover, no noticeable changes in the state or management of the area were observed in the area along the sampling years. Home ranges of pumas in the study area vary between 19 and 84.5 km^2 (Barrera et al. 2010, see also Franklin et al. 1999) and remain in their home ranges year-round (Franklin et al. 1999). We thus considered winter surveys as a valid proxy of puma relative occurrence during summer. Culpeo fox home ranges in the area vary between 4.5 and 9.8 km^2 (Johnson and Franklin 1994), and are also territorial species. Hence, the same assumption for relative occurrence was applied. We also deployed remote cameras to record predators along the road

network used for guanaco surveys. Specifically, we installed scent-stations (Long et al. 2003) every 5 km (n = 40); each scent station was formed by three scent-points separated each other by 500 m. We used a small synthetic sponge (0.05 m above the ground) soaked with bobcat urine as a lure. We also used footprint traps around scent-points. In addition, at the central scent-point of each scent station, we placed a Cuddeback® Capture IR Digital-camera (Cuddeback® Digital, Non Typical Inc., Park Falls, WI, USA) with the pyroelectric infrared (PIR) motion detection sensor focused to the center of the scent station, where the attractant was located. Each scent station was active 24 hours; this implies 40 camera-trapping nights (plus the corresponding 80 scent points). We combined both sampling methods in order to increase sampling size, finally reaching 49 detections for pumas and 66 for culpeo foxes. We then converted predator records from both surveys into estimates of probability of presence as a proxy of relative occurrence and predator encounter probability. We used MaxEnt software (Phillips et al. 2006; see below) to build models of probability of presence since this software provides a good fit with our type of data (sure presences coming from a combination of snow tracking and camera trapping obtained from an uneven sampling protocol).

Statistical analysis

We used generalized linear mixed models (GLMM) to evaluate the responses of guanaco family groups to variation in both relative predator occurrence and perceived predation risk. We used group size, group cohesion and vigilance as response variables. Group cohesion was calculated as the density of guanacos within a group (number of guanacos/group occupation area; where group occupation area is the area of the rectangle that contained the group in ha.). For group vigilance, we considered the number of vigilant adults in a group. We excluded the number of chulengos as they do not contribute to predator detection. Due to the potential effect of group size on vigilance, we evaluated the role of predator occurrence and perceived predation risk on residual vigilance (vigilance after removing the group-size effect; Supplementary Material 1).

We evaluated each response variable as a function of the following set of explanatory variables related to perceived predation risk: percentage of shrub cover, visibility, conspecific density; and relative puma and culpeo fox occurrences. We analysed the location of the groups to account for potential differences in guanaco behavior related to the protected area (within/outside it). In addition, we included the chulengo/adult ratio as an explanatory variable for group cohesion and vigilance analyses, group size for the group cohesion analysis, and group size and its quadratic term for vigilance analysis. Finally, we included year as a (intercept) random effect. Because of the limited number of groups recorded in areas with low visibility, we grouped medium and low visibility levels for our analysis.

To assess actual predation risk, we built a model aimed at estimating relative occurrence of pumas and culpeo foxes using data from our predator surveys. We built a model for each species using MaxEnt (Phillips et al. 2006). We used presence of either predator as the response variable, and a set of climatic and topographic variables as explanatory variables (Supplementary Material 2 and Table S2). Climatic variables were obtained from WorldClim database and topographic variables from Digital Terrain Model ASTER GDEM (METI & NASA). We used boosted regression trees to reduce the initial number of explanatory variables (Elith et al. 2008) prior to building MaxEnt models (Supplementary Material 2 and Table S3). Similarly, we used all guanaco observations to build a model of relative occurrence of guanacos as a proxy of conspecific density, to determine how it affected perceived predation risk (Tables 1 and 2). We assigned conspecific density in a buffer of 500 m radius around each family group, as guanacos can reliable detect conspecific signals and calls of animals belonging to other groups within this distance (Donadio and Buskirk 2006).

We standardized explanatory variables prior to conducting GLMM. We used GLMM with a Poisson distribution and log link function for group size and vigilance, and LMM with a normal distribution for analysis of group cohesion. We used model averaging (Burnham and Anderson 2002) to estimate contributions of variables across the range of plausible models.

We first built the complete set of possible models and we ranked them according to their AIC values. Then, we selected the plausible ones as those whose AIC weights were included in a 95% confidence interval set of models (for a similar approach, see Whittingham et al. 2005). We then applied model-averaging over the selected set of models, obtaining for each predictor the weighted value of its estimators, the unconditional standard error based on Burnham and Anderson (2004) revised formula and its *z* and *p* values to identify significant effects. We performed our analyses using R packages *lme4* (Bates et al. 2011), *MuMIn* (Barton 2012) and *MASS* (Venables and Ripley 2002).

RESULTS

We observed 314 families of guanacos over the 3 years of study. Family group size ranged from 2 to 60 individuals (mean ± SE = 14.6 ± 0.6 individuals), with a mean of 11 ± 0.5 adults, 0.5 ± 0.1 juveniles, and 3.1 ± 0.2 chulengos.

Variation in group size was explained by an averaged model including one variable significantly associated to occurrence of predators and two to perceived predation risk (Table 3, see also Supplementary Material 3 Table S4). According to the model, observed groups were larger at locations with high occurrence of pumas, and smaller at locations with low visibility and with a higher proportion of shrub cover.

Mean group cohesion was 261.8 ± 866 animals/ha. Group cohesion was explained by an averaged model including two variables significantly associated to occurrence of predators and other two to perceived risk (Table 3, see also Supplementary Material 3 Table S5). According to the model, group cohesion significantly increased with relative occurrence of both pumas and culpeo foxes and decreased with group size and guanaco conspecific density.

Overall, mean group vigilance (of the total number of groups) was 10.20 ± 0.01% of adults and juveniles, which corresponds to an average of 0.95 ± 0.10 vigilant animals per group

(min = 0, max = 13). In addition, 56.4% of groups were not vigilant upon first encounter while 43.6% of the groups contained at least one vigilant individual.

Observed differences in vigilance were explained by a model that included one variable associated to perceived predation risk (visibility), group size and its quadratic term; and guanaco conspecific density at a marginally significant level (Table 3, see also Supplementary Material 3 Table S6). According to the model, vigilance increased in areas of low visibility and with group size, and decreased with the quadratic term of group size and guanaco conspecific density. Residual vigilance was only marginally affected by visibility (Supplementary Material 1 and Table S1).

DISCUSSION

Our results suggest that both predator occurrence and perceived predation risk affect grouping behavior of family groups. Thus, group size was influenced by occurrence of predators and by perceived predation risk associated to habitat structure. Group cohesion was related to both predator occurrence and perceived predation risk related to conspecifics, while vigilance was affected by visibility and group size.

As expected, predator occurrence affected group size and cohesion in guanacos, but contrarily to our predictions it did not affect group vigilance. Specifically, guanaco family group size was positively associated to areas with greater relative puma occurrence, where guanacos may reduce individual predation risk through increases in group size (dilution and confusion effects; Hamilton 1971, Lehtonen and Jaatinen 2016). Predator occurrence may be interpreted as a proxy of predator abundance and probability of encounter with a predator because abundance and occurrence are frequently related in carnivores (Linden et al. 2017), although this entails some uncertainty. Aggregation and changes in prey group size as a response to risk have previously been reported in many herbivores (e.g., Banks 2001, Creel et al. 2014, Moll et al. 2016, 2017). In the case of guanaco, Marino and Baldi (2014) reported larger families in

284 populations coexisting with pumas than in predator-free reserves. Contrarily, the relative
285 occurrence of culpeo fox, an occasional and opportunistic predator, had no effect on guanaco
286 group size. Hence, these results point to a stronger influence of the main predator (puma) on
287 guanaco grouping behavior. Moll et al. (2016) reported similar results for African ungulates,
288 and suggested that differences were likely related to the lethality and hunting-efficacy of each
289 predator. In addition, guanacos exhibited increased group cohesion as a response to an
290 increased occurrence of both pumas and culpeo foxes. Increasing group cohesion may improve
291 early detection of an approaching predator and thus provide guanacos with longer response
292 time (Taraborelli et al. 2012). Thus, guanacos likely benefit from forming large and cohesive
293 groups with increased detection of predators (collective vigilance hypothesis; Pulliam 1973,
294 Pulliam and Caraco 1984, Taraborelli et al. 2012).

295 Perceived predation risk partially affected guanaco group size, cohesion and vigilance.
296 As expected, group size of guanacos was larger in open habitats with high visibility. This is
297 related to resource distribution (Jarman 1974) and to increased conspecific detection in open
298 areas (Gerard and Loisel 1995, Pays et al. 2007). Moll et al. (2016) found similar effect sizes of
299 habitat openness and predation risk in African ungulates, pointing to the important
300 contribution of perceived risk on ungulate behavior (Moll et al. 2017). Acebes et al. (2013) also
301 reported a similar pattern in the Argentinean Monte Desert, where food resources are
302 extremely scarce. There, family groups of guanacos selected open low-risk, less productive
303 areas during the breeding season. These results point to an evolutionary fixed pattern in the
304 species: prioritization of reducing predation risk in the birthing period over the selection of
305 areas with abundant food resources.

306 Group cohesion increased with a decrease in both group size and conspecific density,
307 suggesting a “safer-feeling effect” on guanaco behavior: an increased perception of predation
308 risk when group members are sparsely distributed and/or groups are isolated (Peacor 2003).
309 Contrary to our expectations, shrub cover and visibility did not increase group cohesion. In this

310 case, intra-group competition for resources (interference competition) could constrain family
311 group size and distance among individuals, thus preventing the formation of large and
312 cohesive groups in these habitats (Jarman 1974, Marino 2010). Thus, habitat structure and
313 forage quality and availability may have influenced grouping behavior in guanacos together
314 with perceived predation risk (Ripple and Beschka 2003, Creel et al. 2014, Moll et al. 2016).

315 The number of vigilant individuals was primarily affected by group size but also
316 increased in areas with lower visibility. Neither predator occurrence nor the chulengo/adult
317 ratio were included in top models explaining the number of vigilant individuals within groups.
318 The strong influence of group size on vigilance points to the effect of "collective vigilance", one
319 of the classical hypothesized benefits of living in groups (Pulliam 1973, Pulliam and Caraco
320 1984, Taraborelli et al. 2012). According to the collective vigilance hypothesis, individuals can
321 reduce the time spent in vigilance (and feed more), because in groups, vigilance is equivalent
322 to or greater than a lone individual could afford to engage in. The inclusion of the quadratic
323 term with negative estimator thus points to this release of vigilance allotment by individuals in
324 larger groups. In this sense, the relationship between group size and number of vigilant adults
325 was expected. The lack of relevant predictors explaining variation in residual vigilance
326 (variation in vigilance unaccounted by variation in group size; Supplemental Material 1) could
327 suggest that vigilance in guanaco is a variable directly shaped by group size. However, we
328 found different responses for group size and vigilance. We were thus unable to clarify whether
329 residual vigilance was just 'noise' or responded to other ecological factors, such as social
330 monitoring, not included in the study. Contrary to our predictions, group cohesion and
331 vigilance were not affected by the chulengo/adult ratio; despite chulengos being the preferred
332 prey. These results could be related to the low time allocated to vigilance by females in family
333 groups, in which the male is the main vigilant (Barri and Fernandez 2011, Marino and Baldi
334 2008). Finally, we did not detect differences in guanaco grouping behaviour associated to their
335 location within or outside Torres del Paine National Park.

Interestingly, group cohesion has been sometimes included as an independent predictor for vigilance and antipredator response analyses (Marino and Baldi 2008, Taraborelli et al. 2012). However, to our knowledge, there are no studies including group cohesion as an anti-predator response variable for carnivore-ungulate systems (see Lima and Dill 1990 or Peacor 2003 for other study systems). Our findings suggest that understanding changes in group cohesion may complement traditional studies only looking at changes in group size as antipredator response, and point to the importance of evaluating multiple responses in order to know species-specific antipredator behavior. Specifically, the response of group cohesion to predator occurrence, conspecific density and group size suggest that guanacos are risk sensitive and may adapt their individual distance to other group members according to actual and perceived predation risk.

In conclusion, our results suggest that grouping behaviour is affected by multiple variables including response to predation risk, and support previous suggestions that no single factor drives ungulate antipredator behavior. Predator occurrence, considered to reflect the predator abundance or probability of encounter with a predator, shaped guanaco grouping behavior, and was approximately 10 times more important than shrub cover, which we considered to reflect the perceived predation risk (Laundré et al. 2001; Moll et al. 2017). However, it did not describe antipredator responses alone, showing the importance of the perceived predation risk as an antipredator behavior driver for ungulates, as reported by Creel et al. (2017). Responses to predation risk were also linked to the occurrence of different predator species, highlighting the importance of considering all predator species in studies aimed at understanding antipredator behavior of ungulates. The evaluation of several response variables contributed to a better understanding of ungulate antipredator grouping behavior. Finally, the observed responses were limited to family groups during the breeding season, and further research is necessary to confirm whether the observed patterns apply to other situations.

362

363 **REFERENCES**

364 Acebes, P., Malo, J. E. & Traba, J. (2013). Trade-offs between food availability and predation
365 risk in desert environments: The case of polygynous monomorphic guanaco (Lama
366 guanicoe). Journal of Arid Environments 97, 136-142.

367 Bank, M. S., Sarno, R. J., Campbell, N. K. & Franklin, W. L. (2002). Predation of guanacos (Lama
368 guanicoe) by southernmost mountain lions (Puma concolor) during a historically
369 severe winter in Torres del Paine National Park, Chile. Journal of Zoology 258, 215-222.

370 Banks, P. B. (2001). Predation-sensitive grouping and habitat use by eastern grey kangaroos: a
371 field experiment. Animal Behaviour 61, 1013-1021.

372 Barrera, K., Soto, N., Cabello, J. & Antúnez, D. (2010). *'El puma. Antencedentes para su*
373 *conservación y manejo en Magallanes'*. (Servicio Agrícola y Ganadero. Punta Arenas).

374 Barri, F. & Fernández, M. (2011). Foraging and vigilance time allocation in a guanaco Lama
375 guanicoe) population reintroduced in Quebrada del Condorito National Park (Córdoba,
376 Argentina). Acta Ethologica 14, 103-107.

377 Barton, K. (2012). MuMIn: Multi-model inference. R package version 1.7. 11.

378 Bates, D., Maechler, M., Bolker, B. & Walker, S. (2011). lme4: Linear mixed-effects models
379 using S4 classes. http://cran.R-project.org/package=lme4. R package version 0.999375-
380 42

381 Burnham, K.P. & Anderson, D.R. (2002). Information and likelihood theory: a basis for model
382 selection and inference. *Model selection and multimodel inference: a practical*
383 *information-theoretic approach*, pp.49-97.

384 Burnham, K. P. & Anderson, D. R. (2004). Multimodel inference understanding AIC and BIC in
385 model selection. Sociological Methods & Research 33, 261-304.

386 Cappa, F., Campos, V., Giannoni, S. & Andino, N. (2017). The effects of poaching and habitat
387 structure on anti-predator behavioral strategies: A guanaco population in a high cold
388 desert as case study. PloS one 12, p.e0184018.
389 Caro, T. M., Graham, C. M., Stoner, C. J. & Vargas, J. K. (2004). Adaptive significance of anti-
390 predator behaviour in artiodactyls. Animal Behavior 67, 205–228.
391 Childress, M. J. & Lung, M. A. (2003). Predation risk, gender and the group size effect: does elk
392 vigilance depend upon the behaviour of conspecifics? Animal Behaviour 66, 389-398.
393 Creel, S. & Winnie, J. A. (2005). Responses of elk herd size to fine-scale spatial and temporal
394 variation in the risk of predation by wolves. Animal Behaviour 69, 1181-1189.
395 Creel, S., Schuette, P. & Christianson, D. (2014). Effects of predation risk on group size,
396 vigilance, and foraging behavior in an African ungulate community. Behavioral Ecology
397 25, 773-784.
398 Creel, S., Dröge, E., M'soka, J., Smit, D., Becker, M., Christianson, D. & Schuette, P. (2017). The
399 relationship between direct predation and antipredator responses: a test with multiple
400 predators and multiple prey. Ecology 98, 2081-2092.
401 Donadio, E. & Buskirk, S.W. (2016). Linking predation risk, ungulate antipredator responses,
402 and patterns of vegetation in the high Andes. Journal of Mammalogy 97, 966-977.
403 Eccard, J. A., Meißner, J. K. & Heurich, M. (2017). European roe deer increase vigilance when
404 faced with immediate predation risk by Eurasian lynx. Ethology 123, 30-40.
405 Elbroch, L. M. & Wittmer, H. U. (2012). Puma spatial ecology in open habitats with aggregate
406 prey. Mammalian Biology-Zeitschrift für Säugetierkunde 77, 377-384.
407 Elith, J., Leathwick, J. R. & Hastie, T. (2008). A working guide to boosted regression trees.
408 Journal of Animal Ecology 77, 802-813.
409 Franklin, W. L. (1982). Biology, ecology, and relationship to man of the South American
410 camelids. Mammalian Biology in South America 6, 457-489.

411 Franklin, W. L., Johnson, W. E., Sarno, R. J. & Iriarte, J. A. (1999). Ecology of the Patagonia
412 puma (Felis concolor patagonica) in southern Chile. Biological Conservation 90, 33-40.
413 Gerard, J. & Loisel, P. (1995). Spontaneous emergence of a relationship between habitat
414 openness and mean group size and its possible evolutionary consequences in large
415 herbivores. Journal of Theoretical Biology 176, 511-522.
416 González, B. A., Palma, R. E., Zapata, B. & Marín, J. C. (2006). Taxonomic and biogeographical
417 status of guanaco *Lama guanicoe* (Artiodactyla, Camelidae). Mammal Review 36, 157-
418 178.
419 Hamilton, W. D. (1971). Geometry for the selfish herd. Journal of Theoretical Biology 31, 295-
420 311.
421 Iranzo, E. C., Traba, J., Acebes, P., González, B. A., Mata, C., Estades, C. F. & Malo, J. E. (2013).
422 Niche Segregation between Wild and Domestic Herbivores in Chilean Patagonia. PloS
423 ONE 8, e59326.
424 Iranzo, E. C., Acebes, P., Estades, C. F., González, B. A., Mata, C., Malo, J. E. & Traba, J. (2017).
425 Diffusive dispersal in a growing ungulate population: guanaco expansion beyond the
426 limits of protected areas. Mammal Research.
427 Jarman, P. (1974). The social organisation of antelope in relation to their ecology. Behaviour
428 48, 215-267.
429 Johnson, W.E. & Franklin, W.L. (1994). Spatial resource partitioning by sympatric grey fox
430 (Dusicyon griseus) and culpeo fox (Dusicyon culpaeus) in southern Chile. Canadian
431 Journal of Zoology 72, 1788-1793.
432 Kie, J. G. (1999). Optimal foraging and risk of predation: effects on behavior and social
433 structure in ungulates. Journal of Mammalogy 80, 1114-1129.
434 Laundré, J. W., Hernández, L. & Altendorf, K. B. (2001). Wolves, elk, and bison: reestablishing
435 the" landscape of fear" in Yellowstone National Park, USA. Canadian Journal of Zoology
436 79, 1401-1409.

437 Lehtonen, J. & Jaatinen K. (2016). Safety in numbers: the dilution effect and other drivers of
438 group life in the face of danger. Behav Ecol Sociobiol 70, 449–458.
439 Lima, S. L. (1995). Back to the basics of anti-predatory vigilance: the group-size effect. Animal
440 Behaviour 49, 11-20.
441 Lima, S. L. & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review
442 and prospectus. Canadian Journal of Zoology 68, 619-640.
443 Linden, D. W., Fuller, A. K., Royle, J. A. & HARE, M. P. (2017). Examining the occupancy-density
444 relationship for a low-density carnivore. Journal of Applied Ecology.
445 Long, E. S., Fecske, D. M., Sweitzer, R. A., Jenks, J. A., Pierce, B. M. & Bleich, V. C. (2003).
446 Efficacy of photographic scent stations to detect mountain lions. Western North
447 American Naturalist 63, 529-532.
448 Lucherini, M. (2016). Lycalopex culpaeus. The IUCN Red List of Threatened Species 2016:
449 e.T6929A85324366.http://dx.doi.org/10.2305/IUCN.UK.2016-
450 1.RLTS.T6929A85324366.en. Downloaded on 25 December 2016
451 Marino, A. (2010). Costs and benefits of sociality differ between female guanacos living in
452 contrasting ecological conditions. Ethology 116, 999-1010.
453 Marino, A. & Baldi, R. (2008). Vigilance patterns of territorial guanacos (Lama guanicoe): The
454 role of reproductive interests and predation risk. Ethology 114, 413-423.
455 Marino, A. & Baldi, R. (2014). Ecological Correlates of Group-Size Variation in a Resource-
456 Defense Ungulate, the Sedentary Guanaco. PloS ONE 9, e89060.
457 Moll, R. J., Killion, A. K., Montgomery, R. A., Tambling, C. J. & Hayward, M. W. (2016). Spatial
458 patterns of African ungulate aggregation reveal complex but limited risk effects from
459 reintroduced carnivores. Ecology 97, 1123-1134.
460 Moll, R. J., Redilla, K. M., Mudumba, T., Muneza, A. B., Gray, S. M., Abade, L., Hayward, M. W.,
461 Millspaugh, J. J. & Montgomery, R. A. (2017). The many faces of fear: A synthesis of the
462 methodological variation in characterizing predation risk. Journal of Animal Ecology.

463 Novaro, A. J., Moraga, C. A., Briceño, C., Funes, M. C. & Marino, A. (2009). First records of
464 culpeo (Lycalopex culpaeus) attacks and cooperative defense by guanacos (Lama
465 guanicoe). Mammalia 73, 148-150.
466 Ortega, I. M. & Franklin, W. L. (1995). Social organization, distribution and movements of a
467 migratory guanaco population in the Chilean Patagonia. Revista Chilena de Historia
468 Natural 68, 489-500.
469 Pays, O., Benhamou, S., Helder, R. & Gerard, J. F. (2007). The dynamics of group formation in
470 large mammalian herbivores: an analysis in the European roe deer. Animal Behaviour
471 74, 1429-1441.
472 Peacor, S. D. (2003). Phenotypic modifications to conspecific density arising from predation
473 risk assessment. Oikos 100, 409-415.
474 Périquet, S., Richardson, P., Cameron, E. Z., Ganswindt, A., Belton, L., Loubser, E. & Dalerum, F.
475 (2017). Effects of lions on behaviour and endocrine stress in plains zebras. Ethology,
476 n/a-n/a.
477 Phillips, S. J., Anderson, R. P. & Schapire, R. E. (2006). Maximum entropy modeling of species
478 geographic distributions. Ecological modelling 190, 231-259.
479 Pisano, E. (1974). Estudio ecológico de la región continental sur del área andino patagónica. II
480 Contribución a la fitogeografía de la zona del Parque Nacional Torres del Paine. In:
481 Anales del Instituto de la Patagonia. pp. 59-104.
482 Pulliam, R. H. (1973). On the advantage of flocking. Journal of Theoretical Biology 38, 419-422.
483 Pulliam, H. & Caraco, T. (1984). Living in groups: is there an optimalgroup size?. Behavioural
484 Ecology: an evolutionary approach.(JR Krebs & NB Davies, Eds.) pp. 122-148. Blackwell
485 Scientific Publications, Oxford.
486 Rey, A., Novaro, A. J. & Guichón, M. L. (2012). Guanaco (*Lama guanicoe*) mortality by
487 entanglement in wire fences. Journal for Nature Conservation 20, 280-283.

488 Rinehart, K. A., Elbroch, L. M. & Wittmer, H. U. (2014). Common biases in density estimation
489 based on home range overlap with reference to pumas in Patagonia. Wildlife Biology
490 20, 19-26.
491 Ripple, W. J. & Beschta, R. L. (2003). Wolf reintroduction, predation risk, and cottonwood
492 recovery in Yellowstone National Park. Forest Ecology and Management 184, 299-313.
493 Schroeder, N. M., Matteucci, S. D., Moreno, P. G., Gregorio, P., Ovejero, R., Taraborelli, P. &
494 Carmanchahi, P. D. (2014). Spatial and Seasonal Dynamic of Abundance and
495 Distribution of Guanaco and Livestock: Insights from Using Density Surface and Null
496 Models. PloS ONE 9, e85960.
497 Tambling, C. J., Druce, D. J., Hayward, M. W., Castley, J. G., Adendorff, J. & Kerley, G. I. H.
498 (2012). Spatial and temporal changes in group dynamics and range use enable anti-
499 predator responses in African buffalo. Ecology 93, 1297-1304.
500 Taraborelli, P., Gregorio, P., Moreno, P., Novaro, A. & Carmanchahi, P. (2012). Cooperative
501 vigilance: The guanaco's (*Lama guanicoe*) key antipredator mechanism. Behavioural
502 processes 91, 82-89.
503 Taraborelli, P., Ovejero, R., Torres, M. M., Schroeder, N., Moreno, P., Gregorio, P., Marcotti, E.,
504 Marozzi, A. & Carmanchahi, P. (2014). Different factors that modify anti-predator
505 behaviour in guanacos (Lama guanicoe). Acta Theriologica, 1-11.
506 Thaker, M., Vanak, A. T., Owen, C. R., Ogden, M. B. & Slotow, R. (2010). Group dynamics of
507 zebra and wildebeest in a woodland savanna: effects of predation risk and habitat
508 density. PloS ONE 5, e12758.
509 Traba, J., Iranzo, E. C., Carmona, C. P. & Malo, J. E. (2017). Realised niche changes in a native
510 herbivore assemblage associated with the presence of livestock. Oikos 126, 1400–
511 1409. doi: 10.1111/oik.04066.
512 Venables, W. N. & Ripley, B. D. (2002). *Modern Applied Statistics with S*. Fourth Edition.
513 Springer, New York. ISBN 0-387-95457-0

514 Vidal, O. J. & Reif, A. (2011). Effect of a tourist-ignited wildfire on Nothofagus pumilio forests at
515 Torres del Paine biosphere reserve, Chile (Southern Patagonia). Bosque 32, 64-76.
516 Whittingham, M. J., Swetnam, R. D., Wilson, J. D., Chamberlain, D. E. & Freckleton, R. P. (2005).
517 Habitat selection by yellowhammers Emberiza citrinella on lowland farmland at two
518 spatial scales: implications for conservation management. Journal of Applied Ecology
519 42, 270-280.
520

521 Table 1. Description of guanaco family group response variables and predictor variables.

Response variables	
Group size	Number of animals in a family group
Group cohesion	Density of guanacos within a group (number of guanacos/ group area)
Vigilance	Number of vigilant adults (with heads up above the shoulder level)
Predictor variables	
Predator occurrence	
Puma occurrence	Relative occurrence of puma derived from MaxEnt probability of presence models
Culpeo fox occurrence	Relative occurrence of culpeo fox derived from MaxEnt probability of presence models
Perceived predation risk	
Zone	Location of the family group within/outisde Torres del Paine National Park
Shrub cover	Percentage of shrub cover within a 50 m radius around the centroid of the group
Visibility	Terrain roughness, presence of rocks or other visual obstacles within a 50 m radius around the centroid of the group
Conspecific density	Guanaco probability of presence according to MaxEnt model around each family group within a 500 m radius
Chulengo/adult ratio	Number of calves regarding adults in a family group

522

523 Table 2. Expected direction of change for each behavioral response with predictor variables for guanaco family groups in summer.

Response variable	Puma occurrence	Culpeo occurrence	Zone[1]	Shrub cover	Visibility	Conspecific density	Chulengo/adult ratio
Group size	+	+	+	-	+	+	
Group cohesion	+	+	+	+	-	-	+
Vigilance	+	+	+	+	-	-	+

524 [1]Zone: within vs outside Torres del Paine National Park. The expected change referred to the location within it.

525

Table 3. Variables (averaged) influencing guanaco family group size, cohesion and vigilance. Model estimates, adjusted standard errors and p-values are presented. Significant p-values are marked in bold.

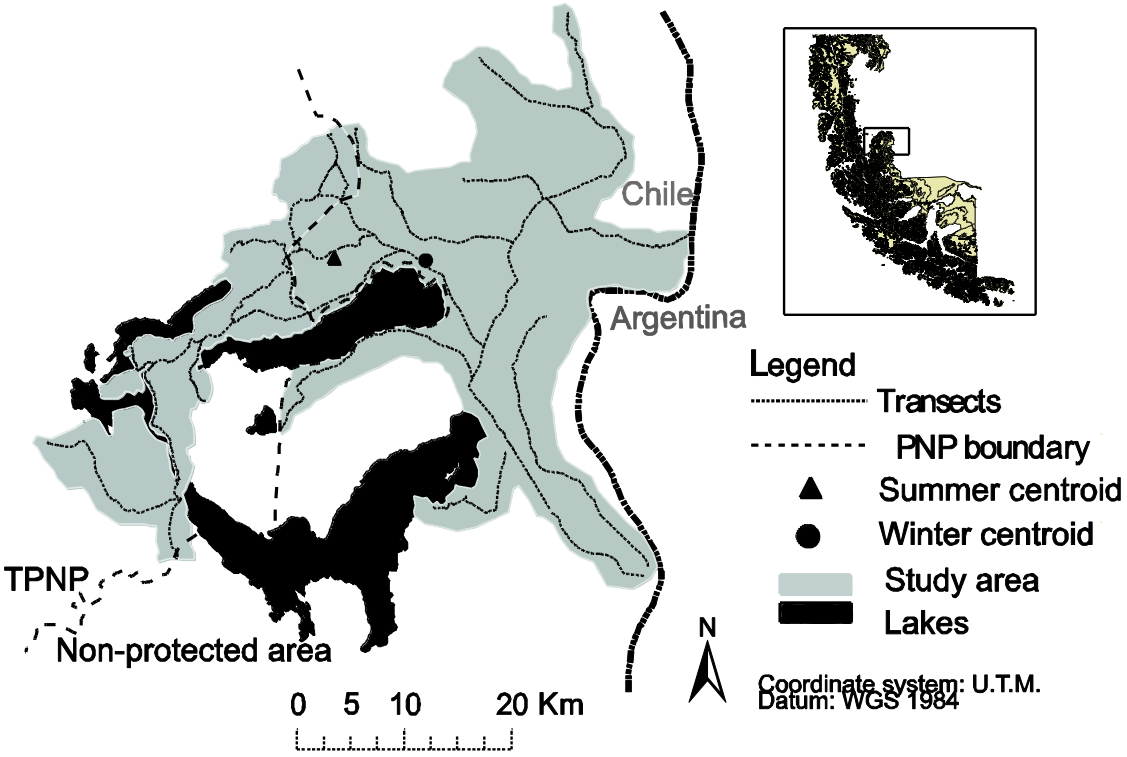
	Group size			Group cohesion			Group vigilance		
	Estimate	Adjusted SE	p-value	Estimate	Adjusted SE	p-value	Estimate	Adjusted SE	p-value
Intercept	2.718	0.061	**<0.001**	-5.086	0.138	**<0.001**	-0.278	0.202	0.170
Puma occurrence	0.143	0.020	**<0.001**	0.426	0.100	**<0.001**	-0.012	0.077	0.874
Culpeo occurrence	0.029	0.018	0.102	0.248	0.096	**0.010**	0.144	0.084	0.086
Zone	-0.018	0.053	0.730	-0.053	0.353	0.880	0.044	0.159	0.782
Shrub cover	-0.085	0.015	**<0.001**	0.095	0.081	0.240	-0.051	0.061	0.404
Visibility	0.187	0.033	**<0.001**	0.045	0.172	0.794	-0.391	0.124	**0.002**
Conspecific density	-0.001	0.020	0.942	-0.468	0.106	**<0.001**	-0.145	0.076	0.057
Group size	-	-	-	-0.372	0.081	**<0.001**	0.466	0.106	**<0.001**
Group size^2	-	-	-	-	-	-	-0.081	0.041	**0.045**
C/A ratio[1]	-	-	-	-0.113	0.080	0.159	0.009	0.060	0.884

[1]C/A ratio = chulengo/adult ratio.

531 **FIGURE CAPTIONS**

532 **Figure 1.** Study area and the road network at the surveyed area in the Comuna Torres del

533 Paine (Magallanes Region, Chile).



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Supplementary Material 1

Residual vigilance is defined as the variation in vigilance unaccounted for by variation in group size. This implies to remove the potential relationship between vigilance ratio and group size. To test residual vigilance, we first fitted a negative binomial regression between the number of scanning adults and the total number of adults per group and its quadratic term. We excluded the number of chulengos as they do not contribute to predator detection. We then used the standardized residuals of this regression as the response variable for the residual vigilance analysis. Residuals provide information about the intensity of group vigilance: positive regression residuals indicate groups more vigilant than the average for that group size, while negative residuals mean under-expected vigilant groups. We used R software to perform analyses.

We evaluated residual vigilance as a function of the following set of explanatory variables related to perceived predation risk: percentage of shrub cover, visibility, conspecific density, chulengo/adult ratio; and relative puma and culpeo fox occurrences. We analysed the location of the groups to account for potential differences in guanaco behavior related to the protected area (within/outside it). We included year as a (intercept) random effect.

We standardized explanatory variables prior to analysis through LMM with a normal distribution. We used model averaging (Burnham and Anderson 2002) to estimate contributions of variables across the range of plausible models. We first built the complete set of possible models and we ranked them according to their AIC values. Then, we selected the plausible ones as those whose AIC weights were included in a 95% confidence interval set of models (for a similar approach, see Whittingham et al. 2005). We then applied model-averaging over the selected set of models, obtaining for each predictor the weighted value of its estimators, the unconditional standard error based on Burnham and Anderson (2004) revised formula and its *z* and *p* values to identify significant effects. We performed our

analyses using R packages *lme4* (Bates et al. 2011), *MuMIn* (Barton 2012) and *MASS* (Venables and Ripley 2002).

Results

Estimates of the averaged model were marginally significant in the case of visibility, and non-significant in the other cases (Table S1). Residual vigilance showed a moderate increase in areas with high visibility, in relation to perceived predation risk.

Table S1. Variables (averaged) influencing residual vigilance of guanaco family groups. Model estimates, adjusted standard errors, z-values and associated p-values are presented. Significative p-values marked in bold.

	Estimate	Adjusted SE	z-value	p-value
Intercept	-0.404	0.132	3.064	**0.002**
Puma occurrence	-0.042	0.053	0.797	0.425
Culpeo occurrence	-0.011	0.051	0.208	0.835
Zone	0.044	0.111	0.397	0.691
Shrub cover	-0.009	0.049	0.181	0.856
Visibility	-0.184	0.100	1.839	0.066
Conspecific density	-0.023	0.050	0.455	0.649
C/A ratio[1]	0.056	0.050	1.123	0.261

[1]C/A ratio: chulengo/adult ratio.

Supplementary Material 2

Database construction

Initial consideration included 33 environmental variables (see Table S2), number strongly reduced after a pre-selection. All variables have been defined on 174 x 218 pixel raster layers. These spatially explicit data have been developed by projection on UTM datum WGS84 time zone 19 South. The spatial resolution was 500 m in all cases.

The initial variables considered included six topographic variables derived from the ASTER GDEM (METI & NASA) digital terrain model: altitude, gradient and roughness, using the mean and standard deviation of each of these. All spatial analyses employed geoprocessing tools under ArcGIS for Desktop 10.1 (Environmental Systems Research Institute, Redlands, CA). The original resolution of the digital terrain model was 18 m but this was reduced so that all variables would be under the same spatial resolution of 500 m x 500 m. Thus each model took the means and standard deviations as summary variables for each of the 500 m pixels.

The normalized difference vegetation index (NDVI) of both sampling periods July and December were also included (year of these images were conditioned by availability and quality of them, see Table S2). Each index was obtained from MODIS-Terra (MOD13Q1/Terra Vegetation Indices 16 Day L3 Global 250 m SIN Grid V005) images.

Variable selection for modelling

For each model, a correlation analysis was used among the 19 climate variables (WorldClim). We only chose the variables after discarding those with high correlation coefficient ($r>0.7$; Elith et al. 2006; Table S2). To further reduce the number of variables entering the modelling process, we applied a Boosted Regression Trees (BRT) with the remaining variables, in order to

599 decrease the risk of over-parametrization and to obtain more robust and hence trustworthy
600 models. BRTs are most useful for detecting, describing patterns and quantifying the relative
601 importance of independent variables (Elith et al. 2008).

602 The BRT models were adjusted and evaluated with R statistical software (R Development Core
603 Team 2014), using the gbm package (Ridgeway, 2010). Parameter selection followed the
604 suggestions of Elith et al. (2008) and Elith and Leatwick (2013), employing a learning rate of
605 0.005, tree complexity 3 and a training/validation proportion of 0.5.

606 This model required presence and absence records and utilized the whole database (55 and 70
607 presences and 439 and 394 absence records for puma and culpeo, respectively). The model
608 chosen by means of the fitted regression trees and resampling to predict puma and culpeo fox
609 presence gave a good fit with 500 and 700 trees, respectively (AUCpuma ± SE = 0.81 ± 0.0;
610 AUCculpeo ± SE=0.57 ± 0.04). Five of the 14 variables included in the model were chosen for
611 the subsequent construction of the distribution model for Puma and 7 variables were chosen
612 for Culpeo fox (Table S3), following Harrell's rule of thumb (Harrell, 1984) to minimize
613 overfitting. Finally, average Maxent models of predator and prey abundance were also
614 included as variables (Table S3).

615

616 **Modelling species probabiity of occurrence**

617 We used MaxEnt software, version 3.3.3.k to model predator (puma and culpeo fox) and prey
618 (guanaco and cattle) distribution. This method only works with presence records. Different
619 models were first compared using ENMTools, varying some of the algorithm parameters
620 including the regularization parameter (Radosavljevic et al. 2014) together with the
621 environmental variable functions (Merow et al. 2013). We compared two different sets of
622 feature classes using the default “autofeatures” option (that allows all possible features),

623 allowing only linear, quadratic and product (LQP) features. The best fitting model was selected
624 using ENM Tools, which enables comparisons via Akaike Information Criterion (AIC) models
625 with different fit parameters (Warren et al. 2010, Warren & Seifert 2011). The best selected
626 model was constructed via 10-fold cross-validation.

627

628 **References**

629 Elith, J., Graham, C. H., Anderson, R. P., Dudı´k, M., Ferrier, S., Guisan, A., Hijmans, R. J.,
630 Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A.,
631 Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. McC., Peterson, A. T.,
632 Phillips, S. J., Richardson, K. S., Scachetti-Pereira, R., Schapire, R. E., Sobero´n, J.,
633 Williams, S., Wisz, M. S. and Zimmermann, N. E. (2006). Novel methods improve
634 prediction of species' distributions from occurrence data. Ecography, 29: 129-151

635 Elith, J., Leathwick, J. R., & Hastie, T. 2008. A working guide to boosted regression trees.
636 Journal of Animal Ecology, 77(4), 802-813.

637 Elith, J., & Leathwick, J. (2013). Boosted Regression Trees for ecological modeling. Tutorial,
638 July, 8.

639 Harrell, F.E. (1984). Regression modelling strategies for improved prognostic prediction.
640 Statistics in Medicine, 3, 143–152.

641 Merow, C., Smith, M.J., & Silander, J.A. (2013). A practical guide to MaxEnt for modeling
642 species' distributions: what it does, and why inputs and settings matter. Ecography, 36,
643 1058-1069.

644 Radosavljevic, A., & Anderson, R.P. (2014). Making better Maxent models of species
645 distributions: complexity, overfitting and evaluation. Journal of Biogeography, 41, 629-
646 643.

647 Ridgeway, G., (2010). gbm: Generalized Boosted Regression Models.

Warren, D.L., Glor, R.E. & Turelli, M. (2010). ENMTools: a toolbox for comparative studies of environmental niche models. Ecography, 33, 607–611. doi: 10.1111/j.1600-0587.2009.06142.x

Warren, D.L. & Seifert, S.N. (2011). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecological Applications, 21, 335-342.

Wellenreuther, M., Larson, K.W., & Svensson, E.I. (2012). Climatic niche divergence or conservatism? Environmental niches and range limits in ecologically similar damselflies. Ecology, 93, 1353-1366.

Table S2. List of initial covariates used to build MaxEnt models for each species (puma and culpeo fox). Selected climatic variables after discarding those with high correlation coefficient (r>0.7) are marked with and asterisk. Basic data for variables introduced in Boosted Regression Trees are included.

	Variables		units	Range in Study Area		
				Mean (±sd)	Max.	Min.
Topographic	Mean altitude		m	557.6(±446.9)	3186.6	0
	standard deviation of altitude			36.5(±51.4)	1636.7	0
	Mean gradient		%	15.4(±9.3)	69	0
	standard deviation of gradient			8.2(±4.1)	38.4	0
	Mean roughness		%	13.3(±5.4)	38.9	0
	standard deviation of roughness			8(±3)	25.3	0
Location	Distance to protect area		m	11032.4(±13215.2)	53649.3	0
	Distance to water bodies		m	5164.1(±6320)	33712.0	0
	Distance to hydrographic network		m	5142.5(±5873.7)	38833.0	0
	Distance to settlements		m	8006.6(±7623.3)	42405.8	0
Climatic	Annual Mean Temperature	Bio1*	ºC	4.4(±2.4)	8.0	-5.1
	Mean Diurnal Range (Mean of monthly (max temp - min temp))	Bio2*	ºC	8.9(±0.5)	10.0	7.5
	Isothermality (Bio2/Bio7)	Bio3*	-	0.5(±0.01)	0.5	0.46
	Temperature Seasonality (standard deviation)	Bio4*	ºC	3.5(±0.27)	4.0	2.8
	Max Temperature of Warmest Month	Bio5				
	Min Temperature of Coldest Month	Bio6				
	Temperature Annual Range (BIO5-BIO6)	Bio7*	ºC	18.4(±1.2)	20.6	15.5
	Mean Temperature of Wettest Quarter	Bio8				
	Mean Temperature of Driest Quarter	Bio9*	ºC	5.3(±3.6)	10.3	-8.7
	Mean Temperature of Warmest Quarter	Bio10				
	Mean Temperature of Coldest Quarter	Bio11				
	Annual Precipitation	Bio12*	mm	823.9(±380.8)	1719	289
	Precipitation of Wettest Month	Bio13				
	Precipitation of Driest Month	Bio14				
	Precipitation Seasonality (Coefficient of Variation)	Bio15				
	Precipitation of Wettest Quarter	Bio16				
	Precipitation of Driest Quarter	Bio17				
	Precipitation of Warmest Quarter	Bio18				
	Precipitation of Coldest Quarter	Bio19				

Vegetation	Mean NDVI December 2012	$NDVI_{Mean12}$	(-1 to 1)	0.37(±0.27)	0.95	-0.19
	Standard deviation of NDVI Dec. 2012	$NDVI_{SD12}$		0.05(±0.05)	0.42	0
	Mean NDVI July 2013	$NDVI_{Mean13}$		0.23(±0.24)	0.98	-0.19
	Standard deviation of NDVI July 2013	$NDVI_{SD13}$		0.06(±0.07)	0.49	0

663

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665

666

667 Table S3. Final set of included and selected (+) variables used to build MaxEnt models for each
668 species (puma and culpeo fox) after applying the boosted regresion tree. The average
669 Maxent models of predator and prey occurrence were also included as variables to
670 build MaxEnt models for each predator species.

Variables			Puma	Culpeo
Topographic	standard deviation of altitude			+
	standard deviation of roughness			+
Location	Distance to protect area		+	
	Distance to hydrographic network			+
	Distance to settlements			+
Climatic	Annual Mean Temperature	Bio1		+
	Isothermality (BIO2/BIO7) (* 100)	Bio3	+	
	Temperature Seasonality (standard deviation *100)	Bio4	+	
	Mean Temperature of Driest Quarter	Bio9	+	
Vegetation	Mean NDVI December 2012	NDVI		+
	Standard deviation of NDVI July 2013		+	+
Prey relative occurrence	Average of Guanaco relative occurrence		+	+
	Average of Cattle relative occurrence		+	+
Predator relative occurrence	Puma average relative occurrence			+

671

672 **Supplementary Material 3**

673 Table S4. Results of the multimodel inference (model averaging) for guanaco family group size,
674 giving details of all models having ΔAIC<10[a]. For model averaging we used models having AIC
675 weights included in a 95% confidence set of models. X indicates the inclusion of the variable in
676 each individual model.

Model	Puma occurrence	Culpeo occurrence	Zone	Shrub cover	Visibility	Conspecific density	AIC	ΔAIC[a]	*wi*[b]
1	X	X		X	X		3445.76	0	0.29
2	X			X	X		3446.48	0.72	0.2
3	X	X	X	X	X		3447.35	1.59	0.13
4	X	X		X	X	X	3447.53	1.77	0.12
5	X			X	X	X	3448.19	2.43	0.09
6	X		X	X	X		3448.46	2.69	0.08
7	X	X	X	X	X	X	3449.24	3.48	0.05
8	X		X	X	X	X	3450.19	4.43	0.03

677 a The difference in AIC values compared with the most economical model (the first model).
678 b Akaike weights.

Table S5. Results of the multimodel inference (model averaging) for guanaco family group cohesion, giving details of all models having ΔAIC<10[a]. For model averaging we used models having AIC weights included in a 95% confidence set of models. X indicates the inclusion of the variable in each individual model.

Model	Puma occurrence	Culpeo occurrence	Zone	Shrub cover	Visibility	Conspecific density	Group size	Chulengo/adult ratio	AIC	ΔAIC[a]	*wi*[b]
1	X	X				X	X		1101.03	0	0.35
2	X					X	X		1103.03	1.99	0.13
3	X	X	X			X	X		1103.68	2.64	0.09
4	X	X				X	X	X	1104.41	3.37	0.07
5	X	X			X	X	X		1104.77	3.74	0.05
6	X	X		X		X	X		1105.04	4	0.05
7	X		X			X	X		1105.44	4.41	0.04
8	X					X	X	X	1106.08	5.05	0.03
9	X				X	X	X		1106.39	5.36	0.02
10	X			X		X	X		1106.51	5.48	0.02
11	X	X	X			X	X	X	1107.03	6	0.02
12	X	X	X		X	X	X		1107.39	6.35	0.01
13	X	X	X	X		X	X		1107.68	6.65	0.01
14		X	X			X	X		1107.92	6.88	0.01
15	X	X			X	X	X	X	1108.14	7.1	0.01
16	X	X		X		X	X	X	1108.22	7.19	0.01
17	X		X			X	X	X	1108.57	7.54	0.01
18	X	X		X	X	X	X		1108.77	7.73	0.01
19	X		X		X	X	X		1108.88	7.85	0.01
20	X		X	X		X	X		1108.95	7.92	0.01
21	X			X		X	X	X	1109.35	8.31	0.01
22	X				X	X	X	X	1109.41	8.38	0.01

23	X			X	X	X	X		1109.86	8.83	0
24		X	X			X	X	X	1110.25	9.22	0
25	X	X	X		X	X	X	X	1110.73	9.69	0
26	X	X	X	X	X	X	X	X	1110.85	9.82	0

a The difference in AIC values compared with the most economical model (the first model).

b Akaike weights.

683 Table S6. Results of the multimodel inference (model averaging) for vigilance of guanaco family group, giving details of all models having ΔAIC<4[a]. For model

684 averaging we used models having AIC weights included in a 95% confidence set of models. X indicates the inclusion of the variable in each individual model.

Model	Puma occurrence	Culpeo occurrence	Zone	Shrub cover	Visibility	Conspecific density	Group size	Group size^2	Chulengo/adult ratio	AIC	ΔAIC[a]	*wi*[b]
1		X			X	X	X	X		951.49	0	0.1
2		X		X	X	X	X	X		952.83	1.34	0.05
3		X	X		X	X	X	X		953.4	1.91	0.04
4	X	X			X	X	X	X		953.42	1.94	0.04
5		X			X	X	X	X	X	953.45	1.96	0.04
6					X	X	X	X		953.67	2.18	0.03
7					X		X	X		953.7	2.21	0.03
8		X			X	X	X			954.1	2.61	0.03
9		X	X	X	X	X	X	X		954.71	3.22	0.02
10	X	X		X	X	X	X	X		954.71	3.22	0.02
11		X		X	X	X	X	X	X	954.77	3.28	0.02
12		X		X	X	X	X			954.9	3.41	0.02
13		X			X		X	X		955.04	3.55	0.02
14				X	X		X	X		955.21	3.72	0.02
15				X	X	X	X	X		955.29	3.8	0.02
16		X	X		X	X	X	X	X	955.38	3.89	0.01
17	X	X	X		X	X	X	X		955.4	3.91	0.01
18	X	X			X	X	X	X	X	955.4	3.92	0.01

685 a The difference in AIC values compared with the most economical model (the first model). There are 120 models having ΔAIC<10, but their Akaike weights
686 are < 0.01.
687 b Akaike weights.